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A northern population of Willow Tits *Parus montanus* did not store more food than southern ones

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For Willow Tits hoarded food is an important part of the winter diet. A larger supply of stored food should then be required in areas with long and cold winters than in areas with short and mild winters. Since the storing of winter supplies occurs mainly during a few autumn months, it is then plausible that hoarding intensities at that time should be higher in northern than in southern populations. Foraging and food hoarding intensities in Willow Tits were sampled simultaneously with standardized observation methods in the southern, central and northern parts of the species range during the main hoarding period in autumn. However, hoarding intensities were highest in the central, and not as expected in the northern area. The southernmost birds may have stored almost as much food as the birds in northern populations, although the intensity peak came later in autumn. The observed differences in hoarding intensity were probably due to differences in the supply of storable food items, since Willow Tits encountered food at a higher rate in the central than in the other two areas. Eating intensities were similar in all three areas, around 0.8 items per minute, and it seems likely that Willow Tits stored supplementary food after satisfying a maintenance requirement of this magnitude. In the northern area subordinate birds hoarded at a higher rate than dominants, whereas this was not the case further south. It is not intuitively clear why this should be so, but foraging at high intensities may be costly. Subordinate birds have secondary access to food and high mortality during cold winters and might therefore work relatively harder in cold areas to build up winter food supplies.

1. Introduction

Energy reserves allow foragers to survive periods of food scarcity. Hoarding animals store energy either in the form of body fat or as supplies of stored food. In areas with cold winters, many bird species increase the amount of body fat reserves during the winter, so-called winter fattening (e.g. Lehikoinen 1987, Haftorn 1989). In such areas, hoarding species also build up large supplies of stored food during the autumn (Haftorn 1956, Brodin 1994).

Willow Tits are territorial and form small flocks with a linear rank hierarchy during the autumn and winter (Ekman & Askenmo 1984, Hogstad 1988, Koivula & Orell 1988). The species is well suited to investigate latitudinal differences in hoarding behaviour, since it has a geographical extension ranging from the northernmost part of the Eurasian taiga zone down to the coniferous forests of Central Europe. Far north winters are longer and colder at the same time as daylength available for foraging is shorter. We thus hypothesize that individuals in northern populations should store more food in autumn than birds further south. Since the time between breeding and winter also is shorter, this should be reflected in hoarding intensities. In a similar investigation of hoarding Crested Tits *P. cristatus*, birds in central Sweden stored food at higher intensities than birds around Antwerp in Belgium (Brodin et al. 1994).

In this study we compare hoarding intensities between Willow Tit populations in different climatic zones, by simultaneous and standardized observations of naturally foraging birds in the southern, central and northern parts of the species range.

2. Materials and Methods

During the autumn of 1993, we recorded hoarding intensities of free-ranging Willow Tits in coniferous forest areas north-east of Antwerp, Belgium (51°25′N, 4°25′E), near Stockholm, South-central Sweden (59°10′N, 18°20′E, and 59°50′N, 18°30′E) and near Oulu, northern Finland (65°00′N, 25°00′E) (see Orell & Ojanen 1983, Brodin 1992, Lens et al. 1994, for habitat descriptions).

We trapped the birds with mist nets and play-back recordings of Willow Tit song. The birds were individually colour banded, and most of them sexed by wing-length measurements (Haftorn 1982) and aged by rectrix shape (Laaksonen & Lehikonen 1976). Even if exceptions may occur, we assumed that first-year birds are subordinate and adults dominant, since this is normally the case (Ekman & Askenmo 1984, Hogstad 1987, Koivula & Orell 1988).

We observed birds for 60-s observation periods during which we recorded the number of food items eaten and stored. The reasons for the choice of 60-s observation periods are several. Tits are agile birds which frequently disappear out of sight in the trees during foraging which makes it difficult to follow an individual even for 60 s. When encountering a rich food source, the flock often stops to store for a longer period, making them easier to observe. Longer observation periods could emphasize such "high intensity" periods and overestimate storing intensities. To avoid serial correlation, we allowed a minimum of two minutes to pass before a sampled individual could be observed again. During two minutes there is time for many foraging decisions. To avoid detection biases, we did not take any observations until five minutes had passed after encountering a flock. Since hoarding is a very obvious act, which is hard to miss (see Discussion) the risk for differences depending on observers is small.

The peak hoarding period might vary between different latitudes depending on when seeds ripen, winter starts, etc. Judged from earlier observations of hoarding tits, we considered it probable that it would occur in September in Finland and Sweden (Haftorn 1956, own observations) and in late October or early November in Belgium (Lens et al. 1994). To estimate the total hoarding effort, we therefore sampled hoarding in two periods, from 6 September to 1 October (Period 1) and 11 October to 5 November (Period 2).

Our observations were made from 09.30 to 11.30 in the morning and from 13.30 to 15.30 in the afternoon. For each individual bird, we distributed our observations equally between mornings and afternoons. We used mean values for individuals as independent observations, and two-tailed non-parametrical statistical tests.

We obtained data from a total of 93 birds (20 in Antwerp, 36 in Stockholm and 37 in Oulu). Mean number of observation periods per bird was 22.3, 27.0 and 27.7 in the three areas, respectively. In the Antwerp area, where Willow Tits are not as common as further north, we sampled the same 20 individuals in both periods. In the two other areas, most individuals sampled during Period 2 were from different but similar territories. To increase the sample size in Period 2, also some individuals in Stockholm and Oulu were sampled a second time. To ensure that data are independent in the tests of differences between areas, these are either made for each period separately or as means for both periods together. When periods are compared area-wise, this is tested with a paired test (Wilcoxon

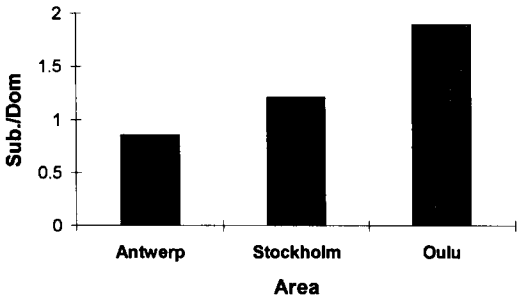

Fig. 1. Ratio between young birds (subordinates) and old birds (dominants) in hoarding intensity. The difference between subordinates and dominants was significant in Oulu (Mann-Whitney test, $z = 2.0$, $n_{sub} = 15$, $n_{dom} = 22$, $p < 0.05$) but not in Stockholm ($z = 1.30$, $n_{sub} = 19$, $n_{dom} = 15$, n.s.) or Antwerp ($z = 0.95$, $n_{sub} = 10$, $n_{dom} = 10$, n.s.).

matched pairs) for Antwerp and with two sample tests (Mann-Whitney) in the two other areas. In the latter test, each individual is only included in the period during which it was observed most frequently.

3. Results

In a pooled comparison of all three areas, hoarding intensities ($x \pm SD$) were similar in the morning: 0.37 ± 0.26, and in the afternoon 0.33 ± 0.30, so morning and afternoon data are analyzed together hence forward.

In the Oulu area, first-year birds hoarded at a significantly higher rate than adult birds, but not in the other areas (Fig. 1).

The mean hoarding intensity differed between areas for the whole study period (Kruskal-Wallis test, $H_2 = 93.0$, $n = 93$, $P < 0.001$), for Period 1 ($H_2 = 27.6$, $n = 59$, $P < 0.001$) and Period 2 ($H_2 = 25.7$, $n = 60$, $P < 0.001$), being higher in Stockholm than in Antwerp and Oulu. The average hoarding intensity of 0.25 in Oulu, however, may be too low to be representative since winter with a lasting snow cover came already on 12 October. Hence the second period in Oulu (mean 0.11) includes many observations during winter conditions (almost no hoarding). The mean from Period 1, 0.37, is probably more representative. In Antwerp the hoarding intensity was higher in Period 2 (Wilcoxon matched pairs, $Z = 2.72$, $n = 20$, $p = 0.007$, for means see Table 1), whereas it was highest in Period 1 in Stockholm (Mann-Whitney test, $Z = 2.07$, $n = 16 + 20$, $p = 0.38$) and Oulu (Mann-Whitney test, $Z = 4.69$, n 0 18 + 19, $p < 0.001$).

Also the encounter rate (items/minute both eaten and hoarded) differed between areas in a similar way as hoarding rates (Kruskal-Wallis test, $H_2 = 12.0$, $p < 0.01$). This also appears to depend on Stockholm intensities being higher than Antwerp and Oulu which were similar (Table 1). The mean eating intensity was around 0.8 in all three areas, although it varied between 0.65 and 0.94 when periods are viewed separately.

Table 1. Mean hoarding, encounter and eating rate (items × min^{-1}) during period I. n is number of individuals. Food encountered is the sum of food hoarded and eaten.

		Hoarding		Encounter		Eating	
Area	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Period 1:							
Antwerp	20	0.19	0.15	1.12	0.32	0.92	0.39
Stockholm	19	0.69	0.34	1.34	0.60	0.65	0.37
Oulu	20	0.37	0.17	1.31	0.29	0.94	0.21
Period 2:							
Antwerp	20	0.30	0.14	1.02	0.18	0.71	0.24
Stockholm	29	0.44	0.25	1.36	0.36	0.92	0.44
Oulu	22	0.11	0.07	0.79	0.21	0.69	0.23
Whole autumn:							
Antwerp	20	0.25	0.12	1.06	0.19	0.81	0.23
Stockholm	36	0.55	0.26	1.35	0.38	0.80	0.42
Oulu	37	0.25	0.17	1.07	0.32	0.82	0.23

4. Discussion

Hoarding intensities did not increase with latitude the expected way, from low in Antwerp, intermediate in Stockholm, to high in Oulu. Instead, intensities were highest in Stockholm and similar in the two other areas. The early winter in Oulu may have decreased hoarding intensities during Period 2, but still hoarding intensities during Period 1 were higher in Stockholm than Oulu. Hoarding may have started before our study in Oulu, but earlier in summer, Willow Tits are breeding and moulting and hoarding intensities are very low (Haftorn 1956, Brodin 1994). High hoarding intensities depend on the access of preferred seeds like hemp nettle *Galeopsis* spp., and juniper *Juniperus communis* (Haftorn 1956, Brodin 1994) which are not ripe until August or September (Lagerberg 1956, Snow & Snow 1988).

Food supply may vary between years in different geographical areas. The intensities recorded in Antwerp and Stockholm, however, are representative for those areas since they are similar to earlier estimates from those areas (Lens & Suhonen, pers. obs., Brodin 1994). The high intensities (about 1 item × min-1) in hoarding Willow Tits reported by Pravosudov (1985) and Alatalo and Carlson (1987) from the same high latitudes as the Oulu study area, suggest that the food supply here may have been unusually low. To check this would require a study over several years.

Seen over the whole period, the eating intensities were very similar in all three areas (0.80–0.83 items /minute), suggesting that (i): this is the long-term eating rate that Willow Tits have to maintain during the autumn, and (ii): observation skills were similar in the three areas, since eating is more difficult to observe than hoarding. Provided that food items of approximately the same size are eaten, our recorded intensities should then hold for a comparison.

First-year birds in the north hoarded at a higher rate than adults, whereas this was not the case further south. In cold winters, survival for subordinates is low (e.g. Ekman & Askenmo 1984, Koivula & Orell 1988), and cold winters prevail in the Oulu area, whereas they are rare around Antwerp. As the encounter rates (food eaten and hoarded) were quite similar in Antwerp and Oulu, this suggests that Willow Tits had to work relatively harder to store food in the northern area. Dominants, that have priority access to food (e.g. Ekman & Lilliendahl 1993) could then afford to invest less in building up energy supplies, something that they have been shown to do with body fat supplies.

The low hoarding intensity in Oulu compared with Stockholm, suggests that there may have been low availability of storable food in the Oulu area. Even if the hoarding and encountering intensities in Oulu and Antwerp are very similar, conditions may be very different. One possibility is that the Oulu birds are restricted by food availability and store as much as they can, while Antwerp birds are foraging in a more relaxed way, still with a long period of hoarding ahead of them. The highest hoarding intensities in Stockholm coincided with intensive storing of hemp nettle nuts (Brodin 1994b), and hemp nettle is not common in the Oulu study area (K. Lahti, own observations).

A hoarding intensity in Antwerp of one item each fourth minute throughout the whole study, means that the large scale autumnal food hoarding reported from northern populations also exists in central Europe. If hoarding may have started before our study in Oulu, it most certainly extended beyond our study period in Antwerp. This means that the total amount of food stored could be comparable between central and northern Europe.

In a similar latitudinal study of Crested Tits in Antwerp and Stockholm, the northern population hoarded at higher intensities (Brodin et al. 1994). Crested Tits, however, almost exclusively stored larvae in both areas. In this study, Willow Tits in the Stockholm area most frequently stored seeds (see Brodin 1994), while we mostly observed larvae to be stored in the other two areas. Hoarding intensities should thus be more comparable between areas in the Crested Tit study.

In conclusion, Willow Tits seemed to store supplementary food after satisfying a requirement of around 0.8 items per minute. Low ranked individuals in a harsh climate (Oulu) may have maximized their storing effort, whereas subordinates in areas with milder climates may have foraged in a more relaxed way. While hoarding intensities did not increase with latitude in the expected way, earlier studies suggest that the intensities we recorded in Oulu may be unusually low for that latitude. Thus, it is still possible that northern populations store more food than southern ones, as suggested by a similar study of hoarding Crested Tits (Brodin et al. 1994).

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Sammanfattning: **Nordliga talltitorna hamstrar ej mera föda än i sydligare populationer**

Hamstrad föda utgör en väsentlig del av vinterdieten för talltita, *Parus montanus*. Ett stort förråd av hamstrad föda bör då vara viktigare i områden med långa, kalla vintrar än i områden med milda vintrar. Eftersom hamstringen av vinterförråd till största delen sker under några korta höstmånader, är det troligt att hamstringsintensiteten vid denna tid är högre i nordliga än i sydliga populationer. Furagerings- och födohamstringsintensiteter samlades under samma tidsperiod in med standardiserade observationsmetoder i tre geografiskt skilda områden. Observationerna gjordes under den huvudsakliga hamstringsperioden, hösten, i en nordlig, en central och en sydlig del av talltitans utbredningsområde. Hamstringsintensiteterna var dock högst i det centrala området, och inte som väntat, längst i norr. Titorna i det sydligaste området kan ha hamstrat nästan lika mycket som i de nordliga populationerna, fast intensitetstoppen inföll senare på hösten. Skillnaderna mellan populationerna berodde troligen på olika tillgång till hamstringbar föda, eftersom fåglarna fann föda oftare i den centrala populationen än i de två andra. Fåglarna åt ungefär lika ofta i alla tre studieområdena, ungefär 0.8 matbitar per minut. Det är därför troligt att talltitor hamstrar överskottsmat efter att ha tillfredsställt ett sådant minimibehov. I det nordligaste området hamstrade ranglägre individer oftare än ranghöga, vilket inte var fallet i de två andra områdena.

References

Alatalo, R. & Carlson, A. 1987: Hoarding-site selection of the Willow Tit Parus montanus in the presence of the Siberian Tit P. cinctus. — Ornis Fennica 64: 1–9.

Brodin, A. 1992: Cache dispersion affects retrieval time in hoarding Willow Tits. — Ornis Scand. 23: 7–12.

Brodin, A. 1994: The role of naturally stored food supplies in the winter diet of the boreal Willow Tit Parus montanus. — Ornis Svecica 4: 31–40.

Brodin, A., Lens, L. & Suhonen, J. 1994: Do Crested Tits Parus cristatus store more food at northern latitudes? — Anim. Behav. 48: 990–993.

Ekman, J. & Askenmo, C. 1984: Social rank and habitat use in Willow Tit groups. — Anim Behav. 32: 508–514.

Ekman, J. B. & Lilliendahl, K. 1993: Using priority to food access: fattening strategies in dominance-structured Willow Tit Parus montanus flocks. — Behav. Ecol. 4: 232–238.

Haftorn, S. 1956: Contribution to the food biology of tits especially about the storing of surplus food. Part IV. A comparative analysis of Parus atricapillus L., P. cristatus L. and P. ater L. — K. Norske Vidensk. Selsk. Skr. 4: 1–54.

Haftorn, S. 1982: Variation in body measurements of the Willow Tit Parus montanus together with a method for sexing live birds and data on the degree of shrinkage in size after skinning. — Fauna Norw. Ser. C: 16–26.

Haftorn, S. 1989: Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. — Wilson Bull. 101: 217–235.

Hogstad, O. 1987: Social rank in winter flocks of Willow Tits Parus montanus. — Ibis 129: 1–9.

Hogstad, O. 1988: Rank-related resource access in winter flocks of Willow Tit Parus montanus. — Ornis Scand. 19: 169–174.

Koivula, K. & Orell, M. 1988: Social rank and winter survival in the Willow Tit Parus montanus. — Ornis Fennica 65: 114–120.

Laaksonen, M. & Lehikoinen, E. 1976: Age determination of Willow and Crested Tits Parus montanus and P. cristatus. — Ornis Fennica 53: 9–14.

Lagerberg, T. 1956: Vilda växter i Norden (pp. 88–91 and 1420–1422). — Esselte, Stockholm.

Lehikonen, E. 1987: Seasonality of daily weight cycle in wintering passerines and its consequences. — Ornis Scand. 18: 216–226.

Lens, L., Adriansen, F. & Dhondt, A. A. 1994: Age-related hoarding strategies in the Crested Tit Parus cristatus: should the cost of subordination be reassessed? — J. Animal Ecology 63: 749–755.

Orell, M. & Ojanen, M. 1983: Breeding biology and population dynamics of the Willow Tit Parus montanus. — Ann. Zool. Fenn. 20: 99–114.

Pravosudov, V. V. 1985: Search for and storage of food by Parus cinctus lapponicus and P. montanus borealis. — Zool. Zh. 64: 1036–1043.

Snow, B. & Snow, D. 1988: Birds and berries, A study of an ecological interaction. — T. and A. D. Poyser, Calton.